OCCASIONAL PAPERS
THE MUSEUM
TEXAS TECH UNIVERSITY

NUMBER 89 4 NOVEMBER 1983

ASPECTS OF THE THERMAL BIOLOGY OF THE BOLSON TORTOISE, GOPHERUS FLAVOMARGINATUS

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There are four extant species of tortoises in North America *(Gopherus agassizii, G. berlandieri, G. flavomarginatus, G. polyphemus). G. polyphemus* inhabits mesic regions of the southeastern United States, but the other three species inhabit xeric regions of the southwestern United States and northern Mexico. Despite the fact that these tortoises are a conspicuous component of their environment, until recently little was known about their thermal biology. Woodbury and Hardy (1948), McGinnis and Voigt (1971), and Voigt (1975) reported thermal values for *G. agassizii*; Judd and Rose (1977) and Voigt and Johnson (1976) reported thermal values for *G. berlandieri*; and Douglass and Layne (1978) reported data accumulated during an 8-year study of *G. polyphemus*. The critical thermal maxima were determined for *G. agassizii* and *G. berlandieri* (Hutchison *et al*, 1966; Brattstrom, 1965; Judd and Rose, 1977). Lowe *et al*. (1971) reported freezing points and supercooling limits of *G. agassizii* and *G. berlandieri*, and Spray and May (1972) reported heating and cooling rates of four species of chelonian, including *G. polyphemus*. No data have been published on the thermal biology of *G. flavomarginatus*.

The bolson tortoise, *G. flavomarginatus*, is the largest terrestrial chelonian occurring naturally in North America. Because of its restrictive range in an inhospitable environment and its secretive behavior, few data have been published on its biology. The species inhabits a limited area of about 10,000 km^2 in northern Mexico (southwest Coahuila, southeast Chihuahua, and northeast

Durango), although its range probably extended into what is now New Mexico and Arizona during the Pleistocene (Auffenberg, 1966).

This large tortoise is similar to *G. polyphemus* and *G. agassizii* in that all three species may construct extensive burrows. These burrows provide protection from unfavorable climatic conditions and from predators and probably are important in reducing evaporative water loss. In addition, the burrow entrance serves as a focal point of courtship activity for *G. polyphemus* (Douglass and Layne, 1978) as well as a primary site of egg-laying.

Two male *G. flavomarginatus* were maintained by the author in an outside enclosure (8 by 18 m) for eight years. In view of the paucity of information concerning the biology of this species, records were maintained of their behavior and body temperatures during this period. Beginning in May 1977, a detailed study of their thermal characteristics was made and the accumulated data form the basis of this report.

Materials and Methods

The two male tortoises used in this study measured 30.0 cm and 32.0 cm total carapace length. They had free access to move inside the enclosure, fed primarily on grasses even though cactus (*Opuntia lindheimeri*) was available, and drank after rains or when the vegetation was watered. The enclosure was shared with numerous adult *G. berlandieri* and one adult female *G. polyphemus*.

The study was begun on 23 May when the tortoises emerged from their burrow and was continued until 16 October 1977 when they retreated for the winter. Temperatures were taken in Celsius, with a Yellow Springs telethermometer, and included the following: body temperature (TB), which was taken through the cloaca at an insertion depth of 8 cm; solar radiation temperature (TAsun), which was taken at a point 8 cm above the ground with the probe fully exposed; and shade temperature (TAshade), which was taken 8 cm above the ground at one of two places, depending on the circumstances. Both shaded areas were extensive and were accessible to the tortoises. Burrow temperature (TAburrow) was taken at a depth of 50 cm with the probe free of the substrate. Time (CDST) was noted when the temperatures were determined.

The tortoise's behavior at the time that the temperatures were taken was divided into five categories: basking, courting (with the female *G. polyphemus*), feeding, walking (but not feeding), and inactive (but not basking).

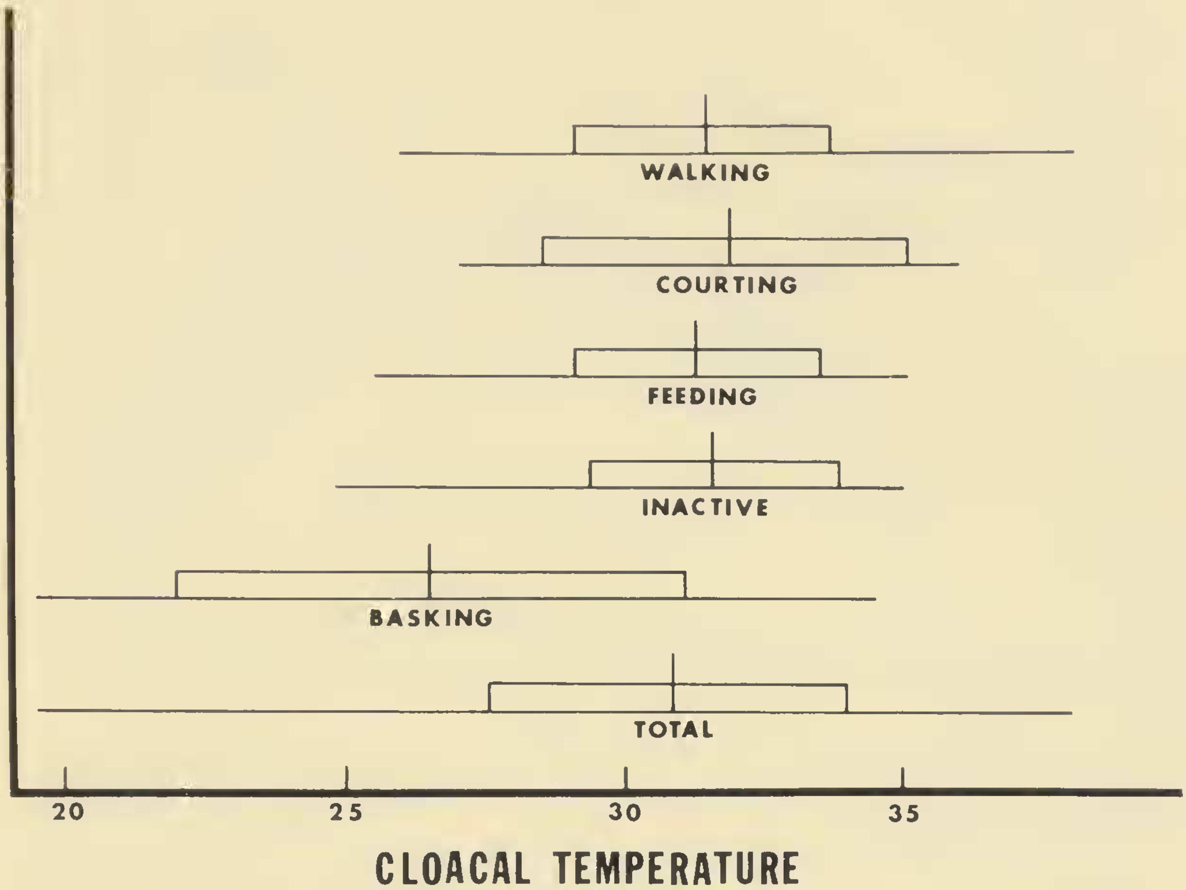

Fig. 1.—Mean, range, and standard deviation of cloacal temperatures (TBs) of *Gopherus flavomarginatus* separated as to behavior.

On 5 June, TB, TAsun, TAshade and TAburrow were recorded beginning at 0845 hrs and continuing approximately each hr until 2230 hrs. The tortoises did not use the burrow on this day but used a large patch of cactus as a thermal shield. TBs were taken regardless of the tortoise's behavior at the designated time.

Data were synthesized and analyzed using SAS through the Texas Tech University Computer Center. Results are expressed as the mean ± standard deviation (range). Differences in means were tested with a one-way ANOVA using an *F*-test. An analysis of covariance was employed to evaluate the slopes obtained when the TBs for before and after 1200 hrs were regressed against TAsun.

Results

The overall mean TB for 181 observations was 30.8±3.2(19.5-38.0) (Fig. 1). If the TBs for basking were eliminated from the calculations, mean TB was 31.5±2.2(24.8-38.0). Only 20 per cent of the observations were below 30°, and the most frequent observations were 32 and 33° (41%). The TB of 38° was unique, and the most frequent observations were 32 and 33°, and no TBs of 36 or 37° were recorded. Only 12 per cent of the observations (excluding basking) were below 33°.

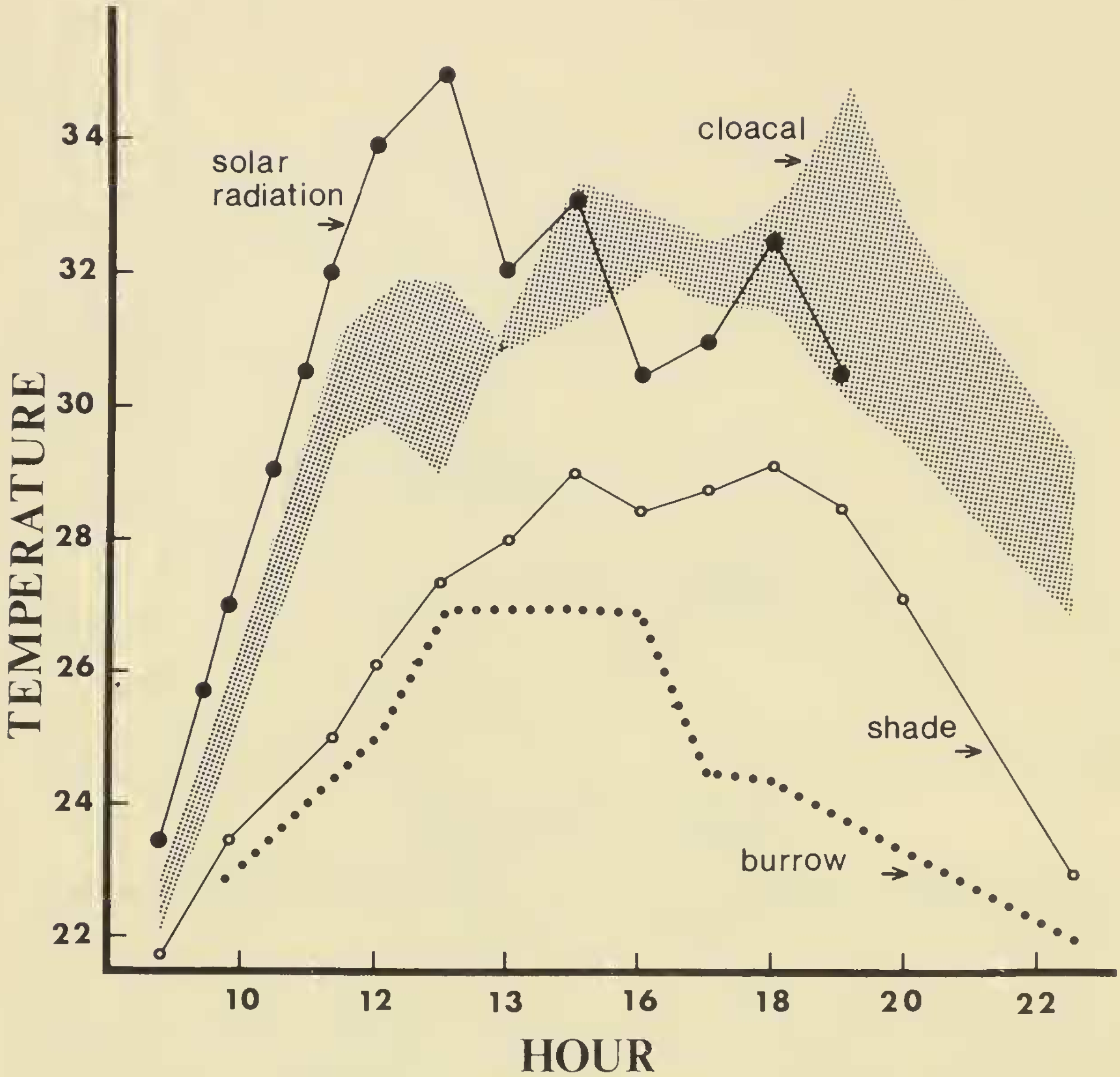

FIG. 2.—Changes in cloacal (TBs), solar radiation (TAsun), shade (TAshade), and burrow temperatures against time of day (CDST).

Generally a tortoise would bask until its TB reached 29-30°. Then it would move either to partial shade, to the burrow, or to the opposite end of the enclosure. When a tortoise remained overnight at the end of the enclosure away from the burrow it could not bask effectively in the morning due to shade and subsequently would move near the burrow to bask.

Mean TB during basking was 26.5±4.6(19.5-34.5). Because basking is a method of elevating TB, TB is a function of the intensity of solar radiation as well as the time spent basking. Thus, in the vast majority of cases the TB measured during basking would have increased had the tortoise's behavior not been altered. To avoid this obvious bias the basking temperatures were eliminated from the calculations unless noted.

Judd and Rose (1977) found no difference between morning and afternoon TBs of *G. berlandieri*. This was not the case for *G. fla-*

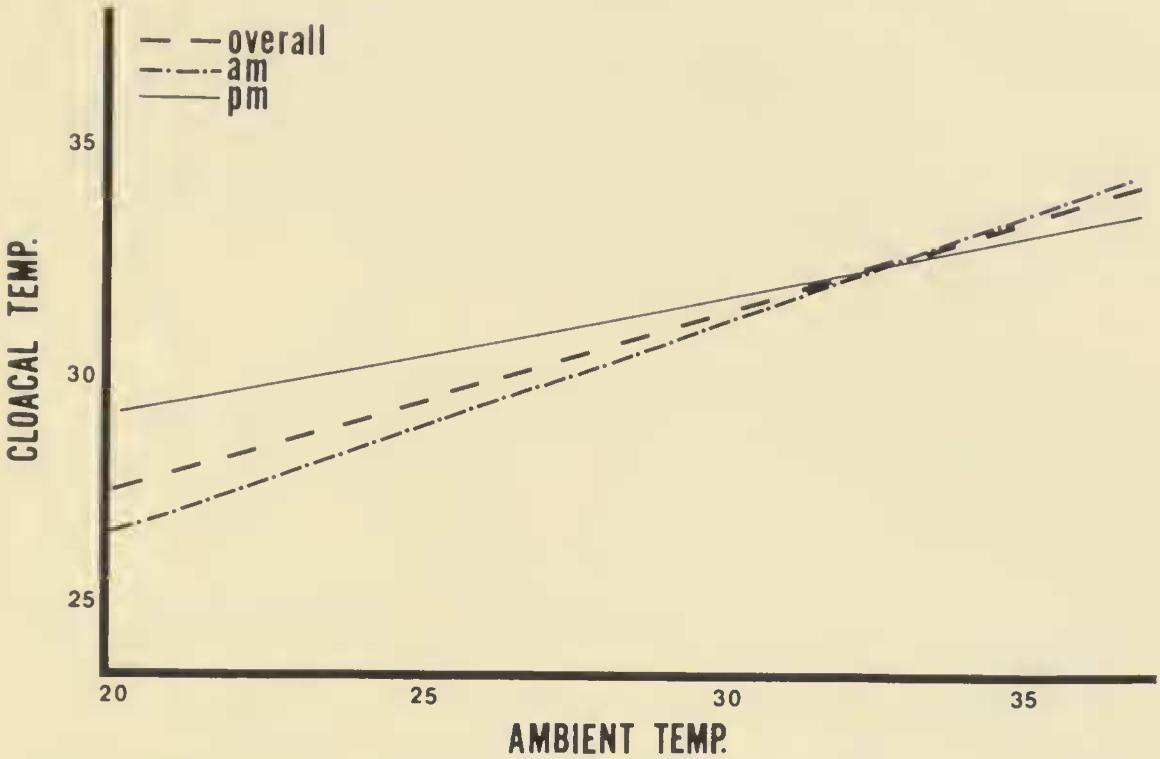

FIG. 3.—Regression lines of cloacal temperatures (TBs) against ambient temperature (TAsun). The three lines represent all of the data, and data collected prior to and after 1200 hrs. Analysis of covariance confirmed that two lines did not significantly enhance interpretation of the data.

vomarginatus for which the mean TB before 1200 hrs was 29.6±1.9 (24.8-32.5); the value after 1200 hrs was 32.2±1.89(25.0-38.0) (F^{1}_{153} = 59.4, $P<0.0001$).

Analysis of covariance confirmed that the overall TB data were positively correlated with TAsun before (F^{3}_{177} = 98.0, $P<0.0001$) and after (F^{3}_{151} = 86.9, $P<0.0001$) the basking temperatures were removed from the calculations (Fig. 2). In the absence of the basking temperatures, the test confirmed that two lines did not significantly (t=1.18, P±0.239) enhance a description of the relationships between TBs before and after 1200 hrs and TAsun.

The tortoises were occasionally observed basking in the afternoon. On 11 such occasions, the TB of a tortoise was ascertained while it fed and again within 30 minutes after feeding, while it basked. The mean TB was significantly higher after feeding: before, $\bar{x}$ = 30.3±1.28(28-32); after, $\bar{x}$ = 33.0±(32-34) (F^{1}_{20} = 32.2, $P<0.0001$).

Mean TBs of tortoises engaged in feeding, walking, courting, or inactivity were not different from overall values or from each other (Fig.1). No tortoise was observed feeding with a TB below 25.5° or courting with a TB less than 27°.

Fig. 3 depicts the relationships between TB, TAsun, TAshade, and TAburrow during a single day. Rate of change for TB and

TAsun was similar in the morning, but as TB neared 30° the tortoises altered their behavior and the hiatus between TAsun and TB increased. As TAsun decreased in the afternoon, the tortoises became more active, more exposed, and their TBs increased to exceed morning post-basking TBs. In fact, TB was highest in the afternoon when TAsun was stable or decreasing.

Comparisons and Discussion

The preferred TB of *G. flavomarginatus* does not appear to differ from that of the other species of *Gopherus* (Table 1). If differences were to be observed, one might expect them to have occurred between *G. polyphemus* and the other three species inasmuch as *G. polyphemus* is the only member of the genus which inhabits mesic areas; or, between *G. berlandieri* and its larger congeners.

Comparisons of the mean TBs of *Gopherus* species and other chelonians are tenuous because there are few terrestrial species of comparable size inhabiting the arid and semiarid regions of North America. *Terrapene ornata* is one of the few, and data have been accumulated on its TB (Fitch, 1956; Legler, 1960). It would appear that this terrestrial emydine has a slightly lower preferred temperature than members of the genus *Gopherus*; however, the important point may be that *T. ornata* is eurythermal in regards to its activity. On overcast days at TAs or TBs below 25°, *T. ornata* may feed actively; *Gopherus* species do not. The herbivorous habit of *Gopherus* may demand high temperatures to facilitate digestion and assimilation of food stuffs.

Burrow temperatures, even in the deserts of the southwest, may be below the optimum temperature needed for proper digestion and assimilation by the tortoises. The observed basking of *G. flavomarginatus* after feeding might represent a behavior to foster digestion. Such a limitation placed on proper digestion may well account for the inordinate amount of time the tortoises spend in and near the burrow entrance.

Hutchison *et al.* (1966) noted that of the 25 species of chelonia tested, the terrestrial testudinids had the highest critical maxima: *G. berlandieri* = 42.8°, *G. agassizii* = 43.1°; and, *G. polyphemus* = 43.9°. The CTM for *G. flavomarginatus* was not determined. However, the combined evidence indicates that the *Gopherus* species are physiologically adapted to comparatively high temperatures.

Differences in TBs of *G. flavomarginatus* prior to and after 1200 hrs are due to differences in TAsun, the large size of the tor-

TABLE 1.—*Summary of the thermal aspects of the four species of* Gopherus. *Modified after Judd and Rose (1977).*

MTB	Min. TB	Max TB	Time	CTM	Freezing point	Super-cooling limit	Source
				Gopherus agassizii			
30.6	19.0	37.8					Brattstrom, 1965
32.3	20.8	38.0	late May				McGinnis and Voigt, 1971
34.7	27.5	38.3	mid July				McGinnis and Voigt, 1971
					—0.95	—4.40	Lowe et al., 1971
				43.1			Hutchison et al., 1966
				Gopherus berlandieri			
31.1	24.1	35.6	Spring				Judd and Rose, 1977
33.1	28.0	39.0	Summer	43.7			Judd and Rose, 1977
				39.0-43.0			Brattstrom, 1965
				42.8			Hutchison et al., 1966
					—0.38	—5.25	Lowe et al., 1971
				Gopherus flavomarginatus			
30.8	19.5	38.0	Spring and				Overall
31.5	24.8	38.0	summer				Excluding basking
				Gopherus polyphemus			
34.7	31.7	38.3	June and				Douglass and
	34.0	35.0	August				Layne, 1978
							Bogert and Cowles, 1947

toises tested, and the corresponding increase in time (due to this size) to attain the preferred temperature for activity. One should expect that the hiatus between pre and post 1200 hrs TBs would be narrower (or eliminated) with smaller tortoises that could warm faster and with individuals inhabiting areas where pre-emergence TB is closer to TAsun. Nonetheless, the differences in mean TB before and after 1200 hrs, after the basking temperatures were removed from the calculations, indicate that time of day at which TBs were determined could influence the mean TB obtained.

Elaborate burrow construction is common to three of the four species of *Gopherus* (although some *G. polyphemus* do not do so, W. Auffenberg, personal communication). The burrows obviously aid individual *G. polyphemus* and *G. agassizii* during cold weather in the northern portions of their ranges, yet burrow construction is also maintained at lower latitudes were TA rarely reaches 0°. In addition, the current range of *G. flavomarginatus* is such that freezing temperatures would occur rarely. It would appear that the burrows provide a thermal shield that protects the tortoises from heat or cold stress. In addition, the burrows provide a primary escape channel of known location during basking, aid in retarding respiratory water loss during basking, provide protection from predators, and form a central focus of activity for certain behaviors such as egg-laying.

In summary, mean TBs of all four species of *Gopherus* appear to be similar (ranging from 30-35°). The long basking time for the large *G. flavomarginatus* accounts for the differences between morning and afternoon mean TBs, which also closely correlate with TAsun.

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ISSN 0149-175X
Texas Tech Press
Lubbock, Texas 79409